

A REVISION OF ACTINOBOLE Fenzl ex Endl. (COMPOSITAE: INULEAE: GNAPHALIINAE)

by

P. S. SHORT *

ABSTRACT

Short, P. S. A revision of *Actinobole* Fenzl ex Endl. (Compositae: Inuleae: Gnaphaliinae). *Muelleria* 6(1): 9-22. (1985). — The endemic Australian genus *Actinobole* Fenzl ex Endl. is revised. Four species are recognised and two of them, *A. drummondiana* P. S. Short and *A. oldfieldiana* P. S. Short, are described as new. The grounds for their delimitation, primarily on anther characteristics and pollen-ovule ratios, are discussed.

INTRODUCTION

In a recent paper (Short, 1981) I suggested that the genus *Actinobole* Fenzl ex Endl., which is confined to Australia, contained only two species, *A. condensatum* (A. Gray) P. S. Short and *A. uliginosum* (A. Gray) H. Eichler. The former species is usually readily distinguished from *A. uliginosum* by having a larger general involucre surrounding the capitula. The leaf-like bracts are c. 1.5-3 times the length of the capitula whereas in *A. uliginosum* they are about the length of the capitula. However within *A. condensatum* two entities were distinguishable on differences in pollen-ovule ratios (P/O's) and anther length. One entity, referred to as an "outbreeder", had an average P/O of 2,037.4. The other entity, an "inbreeder", had an average P/O of 373.1. Since 1981 more collections have been examined, particularly for differences in P/O's and anther characteristics. My results confirm the existence of two entities within *A. condensatum* s. lat. and show that two taxa, similarly differentiated on P/O values and anther size, also exist within *A. uliginosum* s. lat. In this paper I formally give the taxa distinguished on such differences specific status.

MATERIALS AND METHODS

P/O'S AND ANTHER MEASUREMENTS

Only bisexual florets, each with a single ovule, occur in *Actinobole* and thus to determine pollen-ovule ratio's it is only necessary to determine the number of pollen grains per floret. To count pollen indehiscenced, mature anthers were removed from florets and mounted in glycerin jelly containing gentian violet. When squashed, mature anthers readily discharged pollen or else they flattened and thereby allowed all grains to be counted within intact anthers. Initially to determine P/O's all pollen grains were counted in a single floret removed from each of 15 or more individuals of a population. Two or more populations of each taxon were examined. Subsequently P/O's were determined for one or sometimes all individuals from additional collections (populations). All individual counts were combined to give average P/O's for each taxon.

Measurements pertaining to anther characteristics were also initially determined on a population basis and subsequently from one or several individuals from other collections. The measurements used to determine total anther length and the length of the microspor-angia and the terminal anther appendage are depicted in Figure 1. Note that the anther tails are not included in measurements.

Specimens from both herbarium sheets and spirit collections were used for P/O determinations and anther measurements. Collections used for these determinations, at least on a population basis, are mainly housed in AD and MEL. Individuals on herbarium sheets from which a P/O determination and/or anther measurements were made are indicated by a pencilled "P" on the sheet.

CYTOLOGY

Chromosome number determinations were obtained from floral bud material and from root tips. Bud material was fixed, in the field, in 4 parts chloroform: 3 parts absolute ethyl

*National Herbarium of Victoria, Birdwood Avenue, South Yarra, Victoria, Australia 3141.

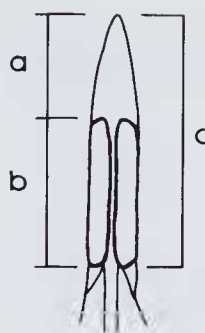


Fig. 1. Anther measurements. a — length of terminal anther appendage. b — length of microsporangium. c — total length of anther.

alcohol: 1 part glacial acetic acid. Root tips were obtained from freshly germinated seed and were fixed in 3 parts absolute alcohol: 1 part glacial acetic acid. Before fixation root tips were placed in a 20 ppm solution of IPC (Storey & Mann, 1967) for two hours. Anther material was stained with aceto-carmin and root tips, following hydrolizing in 1N HCl for ten minutes, were stained with aceto-orcein.

TAXONOMY

Collections have been examined from the following herbaria (acronyms after Holmgren & Keuken, 1974): AD, BM, BRI, CANB, CBG, GH, K, KP (Kings Park, Western Australia), MEL, NSW, NT, PERTH and UWA.

RESULTS

P/O'S AND ANTHER MEASUREMENTS

Table 1. Pollen-ovule ratios and anther characteristics of species of *Actinobole*.

| Characteristic | Species | \bar{x} | S.D. | S.E. \bar{x} | Range | n | Populations |
|--|------------------------|-----------|-------|----------------|-------------|-----|-------------|
| Pollen grains per floret (P/O) | <i>A. drummondiana</i> | 1,944.1 | 366.2 | 49.3 | 1,282-2,876 | 55 | 15 |
| | <i>A. condensatum</i> | 304.2 | 103.4 | 15.09 | 144-508 | 47 | 7 |
| | <i>A. oldfieldiana</i> | 1,336.2 | 204.5 | 22.3 | 730-1,795 | 84 | 25 |
| | <i>A. uliginosum</i> | 110.5 | 31.5 | 1.8 | 36-200 | 307 | 64 |
| Total anther length (mm) | <i>A. drummondiana</i> | 0.95 | 0.072 | 0.01 | 0.8-1.18 | 48 | 10 |
| | <i>A. condensatum</i> | 0.6 | 0.059 | 0.008 | 0.49-0.77 | 51 | 10 |
| | <i>A. oldfieldiana</i> | 0.95 | 0.083 | 0.01 | 0.8-1.15 | 63 | 4 |
| | <i>A. uliginosum</i> | 0.48 | 0.074 | 0.005 | 0.27-0.65 | 205 | 12 |
| Length of microsporangia (mm) | <i>A. drummondiana</i> | 0.7 | 0.065 | 0.009 | 0.59-0.87 | 48 | 10 |
| | <i>A. condensatum</i> | 0.37 | 0.049 | 0.006 | 0.27-0.5 | 51 | 10 |
| | <i>A. oldfieldiana</i> | 0.66 | 0.06 | 0.007 | 0.52-0.86 | 63 | 4 |
| | <i>A. uliginosum</i> | 0.27 | 0.057 | 0.004 | 0.14-0.4 | 205 | 12 |
| Length of terminal anther appendage (mm) | <i>A. drummondiana</i> | 0.25 | 0.039 | 0.005 | 0.2-0.4 | 48 | 10 |
| | <i>A. condensatum</i> | 0.22 | 0.062 | 0.008 | 0.12-0.4 | 51 | 10 |
| | <i>A. oldfieldiana</i> | 0.27 | 0.051 | 0.006 | 0.15-0.42 | 63 | 4 |
| | <i>A. uliginosum</i> | 0.21 | 0.038 | 0.002 | 0.09-0.33 | 205 | 12 |

Measurements are summarised in Table 1 and Figure 2. They are referred to the species ultimately recognised.

In many cases populations within each species, when compared with each other, showed statistically significant differences in the various attributes examined. However population data obtained (housed in MEL) are not presented, as for the purposes of this paper the important factor is that population figures readily form distinct classes which allow the recognition of taxa.

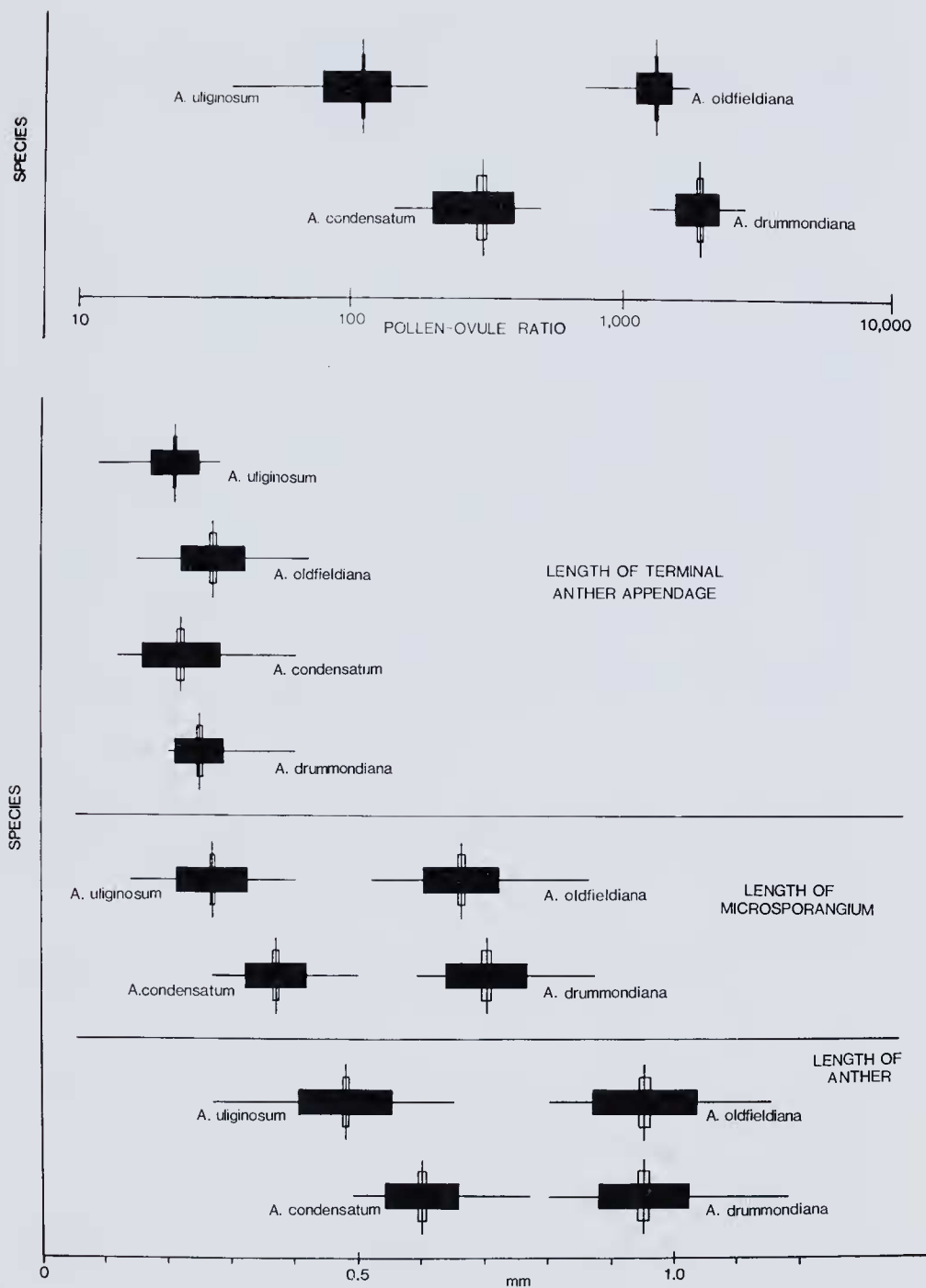


Fig. 2. Pollen-ovule ratios and anther characteristics of species of *Actinobole*.

CYTOLOGY

The only definite chromosome number determination obtained came from *Short 1540*, a collection subsequently referred to as *A. oldfieldiana*. Counts of $n = 11$ were recorded from three plants.

Root tip squashes of *A. uliginosum* s. str., from *Short 827*, were inconclusive. Two determinations, of $2n = c.22$ and $2n = c.24$, were obtained.

DISCUSSION

Cruden (1977) showed that pollen-ovule ratios (P/O's) are a conservative indicator of a flowering plant's breeding system. A number of papers (eg. Lloyd 1965; Cruden 1976a, b; Schoen 1977; Cruden & Hermman-Parker 1979; Spira 1980) support this contention. Within the Compositae they include Baker (1967, *Eupatorium*), Gibbs et al. (1975, *Senecio*) and Lloyd (1972, *Cotula*), although none of these authors actually records P/O's, ascertaining instead the floret sex ratio and/or the number of pollen grains per anther lobe, per anther or per floret. However in all cases it is clear that, if computed, there would be a strong correlation of P/O values with breeding systems. I (Short 1981) have similarly found that closely related species of native Australian Compositae can, on differences in P/O's, readily be classed as 'inbreeders' (i.e. taxa within which plants commonly self-pollinate; referred to herein as selfers or selfing taxa) or 'outbreeders' (i.e. taxa within which plants, although possibly self-compatible, commonly cross-pollinate; referred to herein as outcrossing taxa or outcrossers). In a further paper I (Short 1983) recognised two species of *Chrysocoryne* which, although sometimes differing in habit, were primarily recognised by the number of florets per capitulum, the number of corolla lobes per floret and in particular by anther size and P/O values. More recently Lawrence (1985), following experimental work, has found that P/O's and capitulum morphology reflect whether or not Australian species of *Senecio* are self-compatible or self-incompatible.

Although it may still be argued that more data should be obtained on the use of P/O's in reflecting breeding systems I again give the taxa recognised in this paper specific status because:

1. P/O determinations and anther sizes readily group together into discrete classes which allow the recognition of taxa. Pollen counts and measurements have been taken from a large number of populations and individuals, often scattered over wide areas. For example in *A. uliginosum* s. lat. at least one individual from each Western Australian collection was examined. Within that state all individuals from collections coming from an area between latitudes $c.28^{\circ}\text{S}$. and $c.30^{\circ}\text{S}$., that is the overlap zone of selfers and outcrossers of *A. uliginosum* s. lat., were examined.

Despite the fact that paired selfing and outcrossing taxa are sympatric (but with a narrow overlap), individuals with intermediate P/O values and anther sizes were not detected when the only mixed collections, *Short 559* (*A. uliginosum* s. lat.) and *Short 393* (*A. condensatum* s. lat.), were examined.

2. Other morphological differences apparently exist between taxa and are correlated with changes from high to low P/O values. Thus the selfing entity of *A. uliginosum* occasionally produces 4-lobed florets and not 5-lobed florets. Furthermore the alignment of pollen grains within the microsporangia suggests that the anthers of outcrossing taxa are tetrasporangiate, those of the selfing taxa bisporangiate.

3. The differences between taxa are consistent with those documented for other closely related species with different breeding systems (eg. see Ornduff 1969; Short 1981).

4. Recognition of taxa is easily accomplished under a dissecting microscope at $c.40$ times magnification. At this magnification it is usually a simple matter to discern whether or not there are few or many pollen grains and it is often not necessary to measure anthers. Hence the recognition of species is not impractical.

Thus *A. condensatum* s. lat. is considered to consist of *A. condensatum* (A. Gray) P. S. Short s. str. and *A. drummondiana* P. S. Short whereas *A. uliginosum* s. lat. is considered to consist of *A. uliginosum* (A. Gray) H. Eichler s. str. and *A. oldfieldiana* P. S. Short.

TAXONOMY

Actinobole Fenzl ex Endl., Gen. Pl. Suppl. 3:70 (1843); Walpers, Repertorium botanices systematicae 6:229 (1846); H. Eichler, Taxon 12:295 (1963); H. Eichler, Suppl. to J. Black's Fl. S. Aust. 327 (1965); P. S. Short in Jessop, Fl. Central Aust. 392 (1981); P. S. Short, Muelleria 4:413 (1981). — *Gnaphalodes* A. Gray, Hook. J. Bot. Kew Gard. Misc. 4:228 (1852), *nom. illeg.*, non *Gnaphalodes* Miller, Gard. Dict. Abr. 4th ed. (1754); Benth., Fl. Austr. 3:577 (1867), p.p. (excluding *G. filifolium* = *Siloxerus filifolius*); Benth. in Benth. & Hook. f., Genera Pl. 2:321 (1873); O. Hoffm. in Engl. & Prantl, Naturl. Pflanzenfam. 4(5):195 (1890), p.p.; F. M. Bail., Qd. Fl. 851 (1900); J. Black, Fl. S. Aust. 1st ed. 649 (1929), 2nd ed. 929 (1957); Grieve & Blackall, W. Aust. Wildfls 773, 823 (1975). NEOTYPE: *A. uliginosum* (A. Gray) H. Eichler [see Taxon 12:295 (1963)].

Annual herbs. Stem reduced, with entire plants consisting of a single inflorescence surrounded by a basal rosette of leaves or the stem forming major branches at or near basal nodes; major axes prostrate or ± decumbent, sometimes developing minor shoots, all axes hairy and terminating in an inflorescence. *Leaves* alternate or sometimes appearing opposite, sessile, spatulate or oblanceolate to obovate, tomentose. *Inflorescences* of 1 capitulum or of 2-10(12) capitula in a compact cluster; all inflorescences ± obloid to transversely ellipsoid or broadly depressed to depressed-ovoid and with a general involucre of leaves and leaf-like bracts which are c. the length of or up to c. 3 times the length of the capitula; general receptacle disc-like or slightly branched, hairy. *Capitular bracts* c. 20-30, usually hyaline but with a central green midrib extending for c. $\frac{2}{3}$ - $\frac{3}{4}$ of its length, the upper part of the lamina often constricted or abruptly attenuated above the midrib, occasionally the entire, outermost bracts leaf-like except for a small, hyaline tip. *Outermost bracts* (the majority) ± lanceolate to ovate or ± oblanceolate or ± narrowly obtrullate to obtrullate, the lamina barely constricted or attenuated above the midrib, all bracts united by long hairs along the margins. *Middle bracts* ± oblanceolate to obovate or narrowly obtrullate to obtrullate, the upper part of the lamina (above the midrib) constricted, ± opaque, flat to curved, reflexed, all bracts united by long hairs at the constriction. *Inner bracts* ± oblanceolate to obovate or narrowly obtrullate to obtrullate or elliptic, the upper part of the lamina (above the midrib) constricted, ± opaque, flat to curved, reflexed, the bracts glabrous or with a few long hairs at the base of the constriction, all bracts free. *Partial receptacle* conical, glabrous. *Florets* bisexual, (7)20-50(63) per capitulum; corolla yellow, (4)5-lobed. *Style* branches truncate, with short sweeping hairs, a distinct stylopodium present. *Stamens* 5; anthers with a sterile apical appendage which is ± triangular and with an obtuse apex; microsporangia tailed, endothecial tissue polarized; filament collar ± straight in outline and composed of ± uniform cells and basally not thicker than the filament. *Achenes* ± obovoid, glabrous, brown and with a diaphanous epidermis which swells on wetting, the stylopodium persisting in mature fruit. *Pappus* consisting of (4)5(6) bristles which are fused at the base, each bristle tapering toward the apex and plumose for most of its length, sometimes ending in a shortly stalked, plumose tuft, the bristles c. the length of the floret tube and strongly reflexed when released from the capitulum.

Chromosome numbers: $n = 10, 11$.

TYPIFICATION:

Actinobole Fenzl ex Endl. was described by Endlicher (1843) without reference to a species and the name applied was in a manuscript of Fenzl's (Walpers 1846). The generic description agrees well with the circumscription of *Gnaphalodes* A. Gray which was described in 1852 and included two species, *G. condensatum* and *G. uliginosum*. Subsequent workers (eg. Bentham 1873; Hoffmann 1894) felt that *Actinobole* and *Gnaphalodes* were possibly congeneric but presumably because of doubt over the application of the former name chose the more recent one, *Gnaphalodes*.

Eichler (1963) noted that *Gnaphalodes* A. Gray is illegitimate since it is a later homonym of *Gnaphalodes* Miller. He also found that apparently no specimens annotated as *Actinobole* by either Fenzl or Endlicher exist in Vienna (W) and thus the correct application of the name was still questionable. Despite this Eichler chose *Gnaphalodes uliginosum* as the neotype species of *Actinobole*, making the combination *A. uliginosum* (A. Gray) H. Eichler. As he pointed out, the conservation of *Gnaphalodes* A. Gray against *Gnaphalodes*

Miller and *Actinobole* does not seem warranted. I have since made the combination *A. condensatum* (A. Gray) P. S. Short (Short 1981) and, in this paper, attribute two new species to the genus.

DISTRIBUTION AND ECOLOGY (Fig. 3):

All four species of *Actinobole* occur in Western Australia. Three are restricted to that state but one, *A. uliginosum*, occurs throughout much of central and southern Australia.

All species of *Actinobole* possess an efficient method of achene dispersal. The pappus in all species usually consists of five stiff bristles which, in the intact capitulum, lie parallel to the corolla tube. As the capitular bracts weaken at maturity the pappus bristles suddenly reflex, shooting the fruits from the capitulum and dispersing them around the plant.

Habitat details are outlined under the respective species.

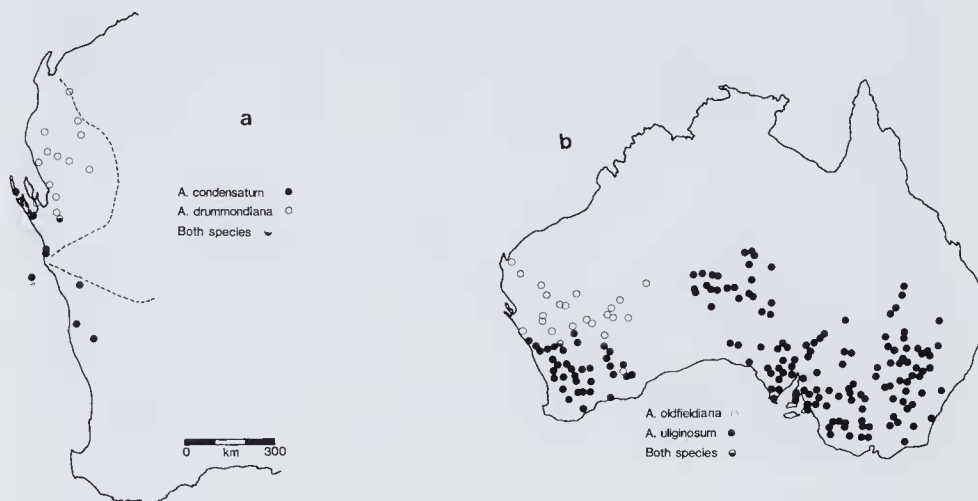


Fig. 3. Distribution of species of *Actinobole*. In fig. 3a the looped broken line represents the approximate western limit of *A. oldfieldiana* and the more or less straight broken line represents the approximate northern limit of *A. uliginosum*.

AFFINITIES /GENERIC CHARACTERISTICS:

Actinobole has commonly been placed in the tribe Inuleae, subtribe Angianthinae (Bentham 1867, 1873; Black 1929). The subtribe was first described by Bentham (1867). Taxa placed in the subtribe were said to be characterised by the possession of tubular, bisexual florets and, most importantly, the presence of "small, sessile or nearly so [capitula] on a common receptacle in dense clusters or compound heads, often closely surrounded by imbricate bracts or by a few floral leaves forming a general involucre" (p. 556).

In more recent times Merxmüller et al. (1977), placing much reliance on pollen structure, stylar structure of bisexual florets and chromosome numbers, suggested that only three subtribes be recognised within the Inuleae. They included the Angianthinae within the Gnaphaliinae, a subtribe incorporating the majority of Australian Inuleae. I agree with this classification. However Merxmüller et al. maintained an "*Angianthus* group" containing all members previously placed in the Angianthinae. As I have previously indicated (Short 1983) the maintenance of such a group is unacceptable. The group is clearly polyphyletic. For example within *Angianthus* s. lat. the majority of segregate genera recognised (Short l.c.) are themselves not obviously related, there being an array of unique bract and achene characteristics which clearly set them apart from one another.

A further problem with using the presence of compound heads as a criterion for grouping genera can be seen in *Actinobole*, *Eriochlamys* Sond. & F. Muell. ex Sond. and *Cephalopterum* A. Gray. Although the majority of individuals in these genera possess several

to many capitula per cluster, in all species there are some individuals with only single capitula.

Despite the above criticism of the use of compound heads in grouping species, their usual presence is a useful, albeit somewhat artificial, character for inclusion in keys. *Actinobole* itself is clearly distinguished from other genera with clustered capitula by the presence of usually five distinctive pappus bristles. Other attributes such as capitular bract morphology and arrangement and achene morphology, alone or in combination, may also be unique to this genus but further work on other members of the Inuleae is required before this can be ascertained.

REPRODUCTIVE BIOLOGY & EVOLUTION:

Pollen-ovule ratios and anther measurements suggest that *A. condensatum* s. lat. and *A. uliginosum* s. lat. each consists of two species. Furthermore the P/O ratios obtained suggest that two species, *A. uliginosum* s. str. and *A. condensatum* s. str. can be regarded as predominantly self-pollinating whereas *A. drummondiana* and *A. oldfieldiana* are more likely to be predominantly cross-pollinated. It also seems possible that the species with low P/O's were directly derived from those species with high P/O's. That is *A. uliginosum* has been derived from *A. oldfieldiana* and *A. condensatum* has been derived from *A. drummondiana*. Such directional changes have been documented for numerous species of flowering plants and are often correlated with other changes related to a plant's reproductive biology (see above discussion; Ornduff 1969; Short 1981).

Chromosome data has been obtained only for three species, *A. drummondiana* ($n = 10$; Turner 1970 as *Gnaphalodes condensatum* A. Gray, voucher T5388), *A. oldfieldiana* ($n = 11$) and *A. uliginosum* ($2n = c. 22$ or $c. 24$). The apparent close relationship with *A. oldfieldiana* suggests that $2n = 22$ is most likely for the latter species. On current knowledge it also seems reasonable to suggest that the ancestral base number is $x = 11$, with aneuploid reduction giving rise to $n = 10$.

I have previously stated that *A. uliginosum* was possibly derived directly from *A. condensatum* s. lat. (Short, 1981). This was suggested on the basis of a generally less conspicuous inflorescence in *A. uliginosum*, its wide geographic distribution and the belief that, unlike *A. condensatum*, *A. uliginosum* consisted only of individuals with low P/O's. The additional data suggests that both *A. condensatum* s. lat. and *A. uliginosum* s. lat. may have been derived from an ancestral, cross-pollinating species (i.e. with a high P/O ratio) with a chromosome number of $n = 11$. Species with different breeding systems, i.e. low P/O's etc., subsequently evolved independently within *A. condensatum* s. lat. and *A. uliginosum* s. lat.

Factors resulting in the evolution of inbreeding and the causes and consequences of inbreeding have been discussed by numerous workers (see Short, 1981 for a brief summary). As all species of *Actinobole* occur in semi-arid and arid regions of Australia pollinator reliability and shorter life cycles are two factors which may be of importance in the evolution of inbreeding in this group.

Ideas relating to the origin of the Australian arid zone flora have been discussed recently by Barlow (1981) and Carolin (1981). Evidence suggests that arid areas, plus an eremean flora, have existed in Australia for at least 15 million years. Some workers (eg. Carolin, l.c.) have even suggested that arid regions have occurred in Australia since the break-up of Gondwanaland.

Although arid areas have existed for long periods of time it is tempting to suggest that both *A. uliginosum* and *A. condensatum* are, geologically speaking, recently derived species. There is an apparent lack of morphological changes (except for the occasional presence of 4-lobed florets and not 5-lobed florets in *A. uliginosum*) accompanying the changes observed in pollen grain number and anther morphology observed within *A. condensatum* s. lat. and *A. uliginosum* s. lat. The cycles of aridity known to have occurred in the past 400,000 years (Bowler, 1981) may have resulted in the change to inbreeding observed not only in *Actinobole* but also in other Australian Gnaphaliinae (Short 1981).

The evolution of chromosome races, often linked with changes in breeding systems, in various species of *Brachyscome* Cass. and *Calotis* R. Br. (Compositae: Astereae) have also been linked with climatic changes in the late Pleistocene and Recent times (Kyhos et al., 1977; Stace, 1981).

KEY TO SPECIES OF ACTINOBOLE

1. Leaves and leaf-like bracts of the general involucre usually c. 1.5-3 times the length (rarely about the length) of the capitula; the upper part of the lamina of the middle capitular bracts narrow and tapering to a \pm acute apex (Fig. 4)
 2. Anthers < 0.8 mm long; pollen grains < 600 per floret and < 100 per anther 1. *A. condensatum*
 2. Anthers > 0.8 mm long; pollen grains > 1200 per floret and > 200 per anther 2. *A. drummondiana*
1. Leaves and leaf-like bracts of the general involucre about the length of the capitula; the upper part of the lamina of the middle capitular bracts \pm rounded at the apex (Fig. 4)
 3. Mature achenes dark green 4. *A. oldfieldiana*
 3. Mature achenes brown
 4. Anthers < 0.7 mm long; pollen grains \leq 200 per floret and \leq 40 per anther 3. *A. uliginosum*
 4. Anthers \geq 0.8 mm long; pollen grains > 700 per floret and > c. 200 per anther .. 4. *A. oldfieldiana*

1. *Actinobole condensatum* (A. Gray) P. S. Short, Muelleria 4:413 (1981). — *Gnaphalodes condensatum* A. Gray, Hook. J. Bot. Kew Gard. Misc. 4:228 (1852); Benth., Fl. Austr. 3:578 (1867); Grieve & Blackall, W. Aust. Wildfls 824 (1975). TYPE: "Swan River, *Drummond*." LECTOTYPE (here designated): *Drummond 863*, *Chrysodiscus* ? Steetz. Pappus equal-eis 5 — apice . . plumosis. Sw. riv., s. dat. (K). SYNTYPES, ISOSYNTYPES OR PROBABLE ISOLECTOTYPES: *Drummond s.n.*, Swan R., s. dat. (GH); *Drummond 363*, s. dat. (BM, MEL).

Annual herb. Stem reduced and unbranched or forming major branches at basal nodes; major axes prostrate to \pm decumbent, 2-5(11) cm long, sometimes developing minor shoots, all axes hairy and terminating in an inflorescence. *Leaves* \pm spatulate or \pm oblanceolate to obovate, 1-3(3.2) cm long, (0.15)0.2-0.5(0.6) cm wide, tomentose, the upper surface less hairy and greener than the grey-green undersurface. *Inflorescences* of 1 capitulum or of 2- c. 20 capitula in a compact cluster, all inflorescences \pm obloid to transversely ellipsoid or broadly depressed to depressed-ovoid, 0.5-1.2 cm high, (0.6)1-1.8 cm diam. and surrounded by a general involucre of leaves and leaf-like bracts, the largest ones c. 1.5-3 times the length of the capitula, rarely about the length of the capitula, all bracts tomentose. *Capitular bracts* 23-28. *Outermost bracts* \pm narrowly obtrullate or \pm oblanceolate, 3.7-6.4 mm long, 0.5-2.1 mm wide. *Middle bracts* \pm narrowly obtrullate to obtrullate or \pm obovate, 4-6.7 mm long, 1.2-2.8 mm wide; upper part of the lamina 1.2-2 mm long, \pm flat, narrow and tapering to a \pm acute apex, yellow or yellow-brown. *Inner bracts* \pm obovate, \pm obtrullate or sometimes \pm elliptic, 4.2-7.7 mm long, 1.3-2.1 mm wide; upper part of the lamina 1.1-1.6 mm long, broader than in the middle bracts, rounded, \pm flat to concave. *Florets* 20-40 per capitulum; corolla tube 2.3-2.8 mm long, 5-lobed. *Stamens* 5. *Anthers* possibly bisporangiate, (0.49)0.55-0.65(0.77) mm long; apical appendage (0.12)0.16-0.35(0.4) mm long. *Pollen grains* (144)160-460(508) per floret, (8)20-80(c. 100) per anther. *Achenes* \pm obovoid, 0.9-1.1 mm long, 0.5-0.6 mm diam. *Pappus* consisting of (4)5(6) bristles fused at the base, each bristle tapering towards the apex and plumose for most of its length but ending in a shortly stalked plumose tuft.

TYPIFICATION:

Gray (1852) described the species of *Gnaphalodes* from collections made by James Drummond in Western Australia and forwarded to Gray by Sir William Hooker. Unfortunately Gray did not record the collection number(s) provided by Drummond although undoubtedly duplicate collections viewed by him and housed in K are numbered. Thus the collection *Drummond 863*, with the name *Gnaphalodes condensatum* apparently in Gray's hand, is regarded as a type collection. I have chosen it as the lectotype because the only material of *G. condensatum* at GH is fragmentary, consisting of florets and capitular bracts contained in a single envelope. Written on the envelope, in Gray's hand, are the words "Gnaphalodes n. gen. Debris examined of the 2 species. Swan R. Drummond." This envelope was contained in a further one with the words, again apparently in Gray's hand, "Gnaphalodes. Gray." Material of both species is generally recognisable and I have sorted and placed the fragments of each species in separate bags within the outer envelope. The syntype collection at GH is regarded as a probable isolectotype.

The collections of *G. condensatum* at BM and MEL can be regarded variously as syntypes, isosyntypes or isolectotypes. They lack any indication that they were examined by Gray and therefore may not be syntypes. However they generally resemble the lectotype

specimen and also have Drummond's original collector's number, 363, attached to them. I suspect that this number should also apply to the lectotype collection at K, a collection which lacks an original collector's tag. In his description in *Flora Australiensis* the only Drummond collection cited by Bentham (1863, p. 578) was 'Drummond, 5th Coll. n. 363', further suggesting that the number '863' was erroneously added to the lectotype sheet.

DISTRIBUTION (Fig. 3):

Confined to Western Australia between latitudes c. 24°S and 30°30' S and west of longitude c. 116°E. It has been collected from several off-shore islands, namely Dirk Hartog Island and North, West Wallabi and East Wallabi Islands in the Houtman Abrolhos. It is partly sympatric with its close relative *A. drummondiana* and a single collection, *Short 393*, containing individuals of both species has been gathered c. 100 km north of the Murchison River bridge along the North West Coastal Highway. Individuals were intermixed, i.e. there were no apparent ecological preferences exhibited by the two species.

ECOLOGY:

A. condensatum tends to grow only in sand. Collector's notes include "In rocky limestone soil", "In sand over limestone, on low heath", "Open scrub . . . *Acacia blakelyi* and *Banksia prionotes*. Soil: deep orange brown sand over limestone", "In red sandy soil with *Eucalyptus loxophleba*", "Growing in white-brown sand in open areas with *Calceophalus francisii* and other herbs between *Carpobrotus*, *Acacia* and other shrubs" and "Low scrub of *Acacia*, proteaceous shrubs and *Labichea*. Deep yellow sand".

SELECTED SPECIMENS EXAMINED (Total c. 21):

Western Australia — Corrick 8133, Kalbarri National Park . . . between Red Bluff and Park boundary, 21.ix.1982 (HO, MEL); George 11409, 5 km N. of C. Ransonnet, Dirk Hartog Island, 2.ix.1972 (PERTH); Griffin 3027 & Blackwell, 20 km SW. of Eneabba, 27.ii.1981 (PERTH); *Short 1604*, c. 3 km SW. of Ardingly, 1.ix.1982 (MEL).

2. *Actinobole drummondiana* P. S. Short, sp. nov.

Ab *A. condensatum* antheris (0.8)0.85-1.1(1.18) mm longis, omnibus flosculis pollinis granis (1,282)1,400-2,600(2,876), omnibus antheris pollinis granis c. 280-520 differt.

HOLOTYPE (Fig. 4c): *Short 417*, Western Australia. c. 28 km S. of Overlander Roadhouse on NW. coastal highway (26°38' S, 114°33' E). Red sand; dominants incl. *Ptilotus obovatus*, *Acacia tetragonophylla* & other *Acacia* sp., 20.viii.1977 (AD 97742617). ISOTYPE: AD (wet colln), MEL, PERTH.

The species is apparently indistinguishable from *A. condensatum* on characters other than those outlined above. Collections of *A. drummondiana* tend to consist of larger, more robust individual specimens than do those of *A. condensatum*. However this is probably just a reflection of sampling and of variable environmental parameters.

A. drummondiana has a chromosome number of $n = 10$ (Turner 1970).

DISTRIBUTION (Fig. 3):

Confined to Western Australia between latitudes c. 22°30' S and c. 27°S and west of longitude c. 115°30' E. (Also see note on distribution under *A. condensatum*).

ECOLOGY:

A. drummondiana appears to grow only in sand. Collectors' notes include "Dry sandy bed of river channel", "Red sand dunes — dominant *Acacia linophylla*", and "Growing in sand in open areas between shrubs of *Hakea*, *Acacia* & chenopods. Associated with various ephemeral herbs including *Gnephosis brevifolia*, *G. gynotricha* and *Pogonolepis* sp.".

NOTE:

1. The specific name commemorates James Drummond. Among his numerous collections are the types of *A. condensatum* and *A. uliginosum*.

SELECTED SPECIMENS EXAMINED (Total c. 22):

Western Australia — Burbidge 6464, Woodleigh Station, 2.ix.1959 (CANB, PERTH); *Short 1552*, c. 1 km

N. of Booloogooro Homestead, 25.viii.1982 (MEL); *Short* 2032, c. 14 km SE. of Carnarvon, 12.x.1983 (MEL); *Turner* 5388, 26 miles E. of Gascoyne Junction, 22.viii.1965 (MEL, PERTH).

3. *Actinobole uliginosum* (A. Gray) H. Eichler, *Taxon* 12:295 (1963); H. Eichler, *Suppl. to J. Black's Fl. S. Aust.* 327 (1965); J. H. Willis, *Handb. Fl. Vict.* 2:732 (1973); Short in Jessop, *Fl. Central Aust.* 392, fig. 504 (1981); Short, *Muelleria* 4:399 (1981); Cunningham, Mulham, Milthorpe & Leigh, *Pl. Western N.S.W.* 711 (1982) — *Gnaphalodes uliginosum* A. Gray, *Hook. J. Bot. Kew Gard. Misc.* 4:228 (1852); Benth., *Fl. Austr.* 3:578 (1867); F. M. Bail., *Qld. Fl.* 851 (1900); J. Black, *Fl. S. Aust.* 1st ed. 649, fig. 306 (1929), 2nd ed. 930, fig. 1232 (1957); Grieve & Blackall, *W. Aust. Wildfls* 823, pl. 13 (1975) p.p. (excluding collections of *A. oldfieldiana*). TYPE: "Swan River, *Drummond*." LECTOTYPE (here designated): *Drummond* 69, Swan River, N. Holl., s. dat. (K). PROBABLE ISOLECTOTYPE: *Drummond* s.n., Swan R., s. dat. (GH). POSSIBLE SYNTYPES OR ISOSYNTYPES: *Drummond* 360, Sw. riv., s. dat. (K); *Drummond* 369 or ?360, s. dat. (BM); *Drummond* s.n., W.A., s. dat. (MEL 83399). See typification, note 1, below.

Gnaphalodes evacinum Sond., *Linnaea* 25:520 (1853); Schdl., *Linnaea* 21:450 (1848), description but no name. TYPE: "Lyndoch-Valley, in solo sterili gregatim crescens, Sept., Octob." LECTOTYPE (here designated): *Mueller* s.n., Lyndoch Valley, s. dat. (GH, ex herb. Sonder, ex herb. Klatt). POSSIBLE ISOLECTOTYPES, SYNTYPES OR ISOSYNTYPES: *Mueller* s.n., Lyndoch-valley, N. Holl. austr., — .ix.1851 (MEL 544152); *Mueller* s.n., In den nördlichen districten stellenweise auf unfruchtbarem boden, oft in dichtgesäeten massen. Sept. Oct. (MEL 84384, ex herb. Sonder); *Mueller* s.n., In . . . madidis . . . arenosis prope Lyndoch valley, — .ix.?1851 (MEL 84321); *Mueller* s.n., Murray, s. dat. (K). See typification, note 2, below.

Annual herb. Stem reduced and unbranched or forming major branches at basal nodes; major axes prostrate to \pm decumbent, c. 1-10 cm long, sometimes developing minor shoots, all axes hairy and terminating in an inflorescence. *Leaves* \pm spatulate or oblanceolate to obovate, 0.3-1(1.3) cm long, 0.15-0.5 cm wide, tomentose, the under surface sometimes more hairy than the upper surface. *Inflorescences* of 1 capitulum or of 2-12 capitula in a compact cluster, all inflorescences \pm obloid to transversely ellipsoid or broadly depressed to depressed-ovoid, c. 0.5-1 cm high, c. 0.6-1.8 cm diam. and surrounded by a general involucre of leaves and c. 15-20 leaf-like bracts which are oblanceolate to obovate, 0.3-0.9 cm long, c. 0.1-0.45 cm wide, the largest ones about the length of the head, all bracts tomentose. *Capitular bracts* c. 19-28. *Outermost bracts* \pm oblanceolate to obovate or \pm obtrullate, sometimes \pm elliptic or \pm ovate, 3.8-4.4 mm long, (0.8)1-1.7 mm wide. *Middle bracts* \pm obtrullate or \pm obovate, 3.7-4.9 mm long, 1.7-2 mm wide; upper part of the lamina 1-1.3 mm long, \pm flat to concave, \pm rounded at the apex, yellow. *Inner bracts* \pm oblanceolate to obovate or narrowly obtrullate to obtrullate, sometimes \pm elliptic, 3.2-4.6 mm long, 1.1-1.8 mm wide; upper part of the lamina (0.5)0.8-1.2 mm long, \pm rounded at the apex, yellow. *Florets* (28)35-55(63) per capitulum; corolla tube 2-2.5 mm long, (4)5-lobed. Stamens (4)5. *Anthers* possibly bisporangiate, (0.27)0.34-0.62(0.65) mm long; microsporangia (0.14)0.16-0.37(0.4) mm long; apical appendage (0.09)0.1-0.25(0.33) mm long. Pollen grains (36)48-180(200) per floret, (4)8-36(40) per anther. *Achenes* \pm obovoid, c. 0.75-0.85 mm long, 0.4-0.45 mm diam. Pappus consisting of 5 bristles fused at the base, each bristle tapering toward the apex and plumose for most of its length, sometimes with a \pm terminal tuft.

Chromosome number: $n = c. 11$.

TIPIFICATION:

1. Gray failed to record Drummond's collection number or numbers in both his publication and on type material (fragmentary and mixed with *G. condensatum* — see under that species) at GH. At K undoubtedly syntype material exists on a sheet containing four separate collections of *A. uliginosum*. Two of these collections were made by Drummond. One of these, *Drummond* 69, consists of a single plant, is labelled in Gray's hand as *Gnaphalodes uliginosum* and must be selected as the lectotype because there is no indication that Gray examined the other Drummond collection, *Drummond* 360. *Drummond* 360 can only be regarded as a possible syntype. I regard the fragmentary material

at GH as a probable duplicate, i.e. an isolectotype, of *Drummond 69*, not of *Drummond 360*.

At BM there is a Drummond collection with an original collector's tag. The number on the tag can be interpreted as either '360' or '369'. It is presumably a duplicate of the K collection labelled, perhaps erroneously, as *Drummond 360*. There is no indication that Gray saw the specimen and thus this collection must be regarded only as a possible syntype or possible isosyntype.

The collection MEL 83399 could perhaps be regarded as an isosyntype or syntype. It contains a number of small plants of *A. uliginosum* and is accompanied by a label with the words "W.A., J. Dr." indicating that it is a collection by Drummond. However the specimens are not a good match with other type material, there is no indication that they were seen by Gray and I think it possible that the label has been erroneously placed with the specimens.

2. Sonder based his description of *Gnaphalodes evacinum* on specimens gathered and sent to him by Mueller. At MEL there are probably three sheets containing type material of *G. evacinum*. The information on one, MEL 544152, complies well with the published notes, giving the location as Lyndoch Valley and the date as September 1851. The label is in Mueller's hand. However there is no indication that this material was examined by Sonder. Another sheet, MEL 84384 (ex herb. Sonder), almost undoubtedly contains type material but unfortunately the labels and specimens on this sheet are mixed. Sonder's handwritten description is placed at the top of the sheet. Below this are two envelopes containing specimens. Only one envelope is labelled, i.e. with Mueller's unpublished manuscript name and the locality "Murray". Two individual plants are mounted below the envelopes and two original labels occur in the bottom right hand corner. One label records "*Gnaphalodes evacinum* Sonder. Murray. Dr. F. Mueller." The other, cited above, records "in the more northern districts, here and there on barren ground, often in densely crowded masses" (English translation by D. Sinkora, 28.vii.1982). The latter label does not record that the specimen comes from the Lyndoch Valley but in other respects the information is more or less in accord with that published by Sonder. The remaining sheet, MEL 84321, also apparently contains mixed labels and specimens. There are two cellophane bags, each containing specimens of *A. uliginosum*. Three labels, not directly referred to the specimens, occur on the sheet. One refers to the Lyndoch Valley collection and is cited above. The remaining labels refer to the locality as the Murray scrub and the date on one is given as October 1848.

Perhaps when describing *G. evacinum* Sonder had material from both the Lyndoch Valley and the Murray scrub. This may well explain the presence of apparently quite different labels on MEL 84321 and MEL 84384. However in the original description there is only reference to the Lyndoch Valley and only this material can be used for purposes of lectotypification. As the labels and specimens are not clearly matched on these two MEL sheets and because there is no indication that the collection MEL 544152 was examined by Sonder, the collection chosen as the lectotype is that held in GH. It consists of two plants, was originally obtained by Klatt from Sonder, and the accompanying label is in Sonder's hand.

Another collection labelled as *G. evacinum* and collected by Mueller from the "Murray" also exists in K and is tentatively considered to be a syntype or isosyntype.

DISTRIBUTION (Fig. 3):

Widely distributed across much of mainland Australia, occurring between latitudes c. 23°S and c. 38°S and west of longitude c. 151°E in central and eastern Australia and in Western Australia south of latitude c. 28°S. It is partly sympatric with its close relative *A. oldfieldiana* and a single collection, *Short 559*, containing individuals of both species has been gathered near Paynes Find, Western Australia.

ECOLOGY:

A. uliginosum occurs in an array of habitats. Collector's notes include "*Acacia aneura* — *Codonocarpus* open woodland on brown-red sand; broad swale between dunes, area surrounding small granite rock. Common in depressions, bare but for small herbs", "As-

sociated with *Acacia aneura* & scattered shrubs on hard, rocky, red clay-loam soil", "In red sand, on low sand hill near clay pan", "Open woodland of *Casuarina* & *Callitris* with scattered *Hakea*", "Growing in granitic depressions with various small annual grasses, composites etc. Sandy loam", "Growing in brown loam amongst *Eucalyptus*, *Acacia* et al shrubs and extending into upper *Arthrocnemum* [= *Halosarcia*] zone around salt lake", "Sandridge dominated by *Dodonaea* & mallee *Eucalyptus*. Associated with grasses & various herbs including *Wahlenbergia*, *Reichardia tingitana*, *Podolepis capillaris*, *Angianthus tomentosus* & *Pimelea trichostachya*", "Low scrub of *Acacia*, Proteaceous shrubs and *La-bichea*. Deep yellow sand" and "Growing in red-brown loam in *Dodonaea* — *Ptilotus* shrubland".

SELECTED SPECIMENS EXAMINED (Total c. 350):

Western Australia — Preiss 2415, Swan River Colony, s. dat. (MEL 84256, MEL 84296); Short 940, Yorkrakine Granite Rocks, 13.xi.1979 (AD); Short 1031, Salt lake c. 21 km N. of Wongan Hills on main road to Kondut, 20.xi.1979 (AD); Short 1606, c. 3 km SW. of Ardingly, 1.ix.1982 (MEL); Short 1760, Eastern edge of Fraser Range, c. 32.5 km west of Newman Rocks turnoff along Western Highway, 19.ix.1982 (MEL).

Northern Territory — Latz 3176, Ooraminna Rockhole, 7.viii.1972 (CANB, NT); Nelson 1734, 1 mile S. Heavitree Gap, 15.viii.1968 (AD, CANB, NT).

South Australia — Barker 3478, c. 10 km NNE. of Mt. Kintore summit, 10.ix.1978 (AD); Short 779, Podinna Rock, 24.ix.1978 (AD); Short 827, c. 6 km SW. of Pt. Julia, 26.x.1978 (AD).

Queensland — Clemens s.n., Charleville, — .ix.1945 (BRI 224710); Pedley 2436, 20 miles W. of Cunnamulla, 8.ix.1967 (BRI).

New South Wales — Corrick 7288, near Mt. Robe, 29.viii.1981 (MEL); Muir 5840, 2 km S. of Tapio Station, 30.viii.1978 (MEL).

Victoria — Corrick 6689, Short & Fuhrer, 30.6 km SE. of Walpeup on road to Patchewollock, 1.x.1980 (MEL); Short 1245, Sandridge above major saline region on western edge of Raak Plain, 27.ix.1981 (MEL).

4. *Actinobole oldfieldiana* P. S. Short, sp. nov.

Ab *A. uliginosum* antheris (0.8)0.85-1.1(1.15) mm longis, omnibus flosculis pollinis granis (730)1,000-1,600(1,795), omnibus antheris pollinis granis c. 200-320 differt.

HOLOTYPE (Fig. 4a): Short 1586, Western Australia. c. 100-150 m above the river bed and c. 400 m downstream of the Murchison River bridge on the North West coastal highway. (27°49' S, 114°40' E). In *Acacia* scrub. Brown loam amongst granite rocks. 31.viii.1982 (MEL). **ISOTYPE**: AD, MEL (wet colln), PERTH.

The species is generally indistinguishable from *A. uliginosum* on characters other than those outlined above. However there are a number of collections, i.e. *Helms* s.n. (AD 96323023, NSW 138815), Barker 2150, Short 515, that are atypical in that the mature achenes are olive green instead of the usual brown. This difference is to some extent correlated with a difference in capitular bract morphology and this correlation is particularly apparent in the *Helms* collections from the Fraser Range (Fig. 4b). On the other hand Short 477, which lacks mature achenes is somewhat intermediate in capitular bract morphology between *Helms* s.n. and typical *A. oldfieldiana*. Further investigations may show that the collections with green achenes should be regarded as a distinct taxon but for the time being they are incorporated under *A. oldfieldiana*.

DISTRIBUTION (Fig. 3):

Restricted to Western Australia between latitudes c. 22°30' S and 29°30' S and west of longitude c. 126°E. (Also see note on distribution under *A. uliginosum*).

The collections with green achenes have a scattered distribution (see list below of specimens examined) and one, *Helms* s.n., from the Fraser Range has a somewhat disjunct distribution when compared with the total distribution of *A. oldfieldiana*.

ECOLOGY:

Few notes on the habitat of *A. oldfieldiana* have been recorded. Collector's notes include "Lateritic outcrop. Growing in rocky places", "Sandy clay flat", "Red loamy soil", "In red loam near creek-line in mulga", "Coarse red sand" and "Open mulga scrub. In loam with ironstone gravel surface".

Individuals with inflorescences consisting of single capitula tend to be more common in *A. oldfieldiana* than in any other species. To some extent this appears to be an envi-

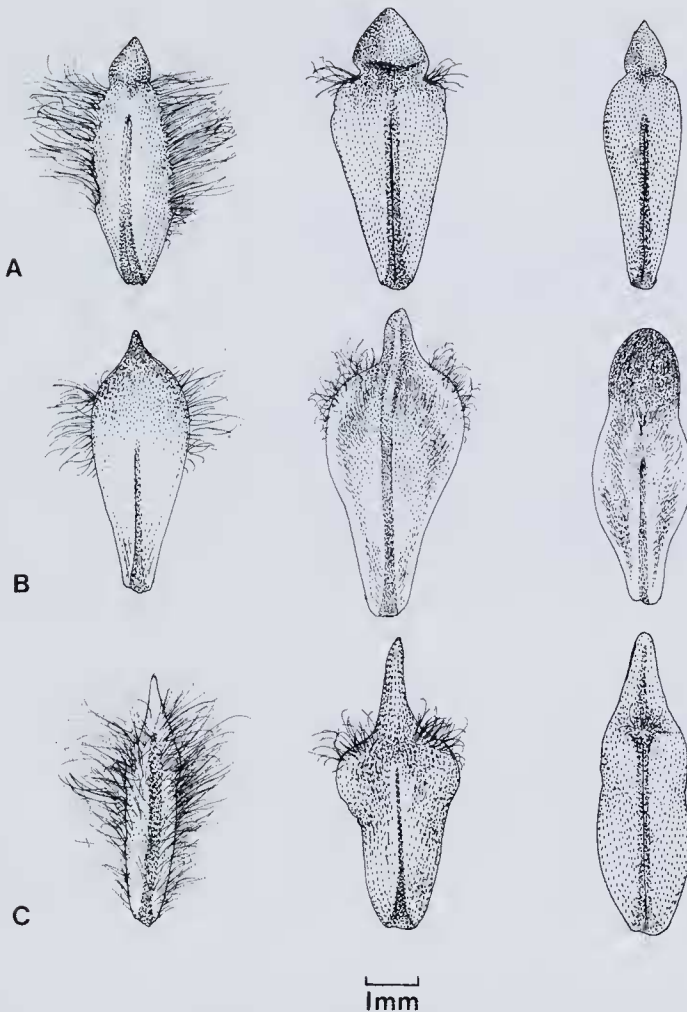


Fig. 4. Capitular bracts (outer, mid & inner) of *Actinobole*. a — *A. oldfieldiana* (Short 1586). b — *A. oldfieldiana* (Helms s.n., NSW 138815). c — *A. drummondiana* (Short 417).

ronmental difference. In the collection *Short 1540* I recorded that single headed specimens grew in the open, the few-headed and less mature specimens in more shaded areas.

NOTE:

1. The species name commemorates Augustus Frederick Oldfield who collected extensively in Tasmania and Western Australia last century.

SELECTED SPECIMENS EXAMINED (Total c. 42):

Western Australia — *Barker 2150*, Yannerie River crossing, Barradale Roadhouse, 30.viii.1977 (AD, green fruit); *Chinnock 730*, 16 km S. of 10 Mile Tank on Bendya — Banjiwarn road, 3.ix.1973 (AD); *Donner 4501*, c. 135 km SW. of Warburton Mission, 30.viii.1973 (AD); *George 5387*, 4 miles E. of Mt. Beadell, 25.viii.1963 (PERTH); *Helms s.n.*, Fraser Range, 4.x.1891 (AD 96323023, NSW 138815, green fruit); *Short 477*, near Lyndon River Homestead, 25.viii.1977 (AD); *Short 515*, c. 1.9 km N. of Errabiddy on main road to Landor homestead, 11.ix.1977 (AD, green fruit); *Short 1540*, c. 18 km from Bandya homestead along road to Laverton, 21.viii.1982 (MEL); *Short 2119*, c. 17 km N. of Murchison River Bridge along the North West Central Highway, 18.x.1983 (MEL).

ACKNOWLEDGEMENTS

My work on Australian Compositae commenced in 1977. Transport and/or funds for field work in Western Australia has been provided by the Botanic Gardens of Adelaide (1977), the Flinders University Research Committee (1979) and Australian Biological Resources Study grants from the Bureau of Flora and Fauna (1982, 1983). Miss A. Podwyszynski provided the illustrations for figure 4.

REFERENCES

- Baker, H. G. (1967). The evolution of weedy taxa in the *Eupatorium microstemon* species aggregate. *Taxon* 16: 293-300.
- Barlow, B. A. (1981). The Australian flora: its origin and evolution. In George, A. S. (ex. ed.), 'Flora of Australia'. (Australian Govt. Publ. Service: Canberra). 1: 25-75.
- Bentham, G. (1867). 'Flora Australiensis' vol. 3. (Reeve: London). Compositae, pp. 447-680.
- Bentham, G. (1873). Compositae. In Bentham, G. & Hooker, J. D., 'Genera Plantarum' vol. 2. (Reeve: London). pp. 163-533.
- Black, J. M. (1929). 'Flora of South Australia' pt. 4, ed. 1. (Govt. Printer: Adelaide). pp. 570-662.
- Bowler, J. M. (1981). Aridity in the late Tertiary and Quaternary of Australia. In Barker, W. R. & Greenslade, P. J. M. (eds), 'Evolution of the Flora and Fauna of Arid Australia'. (Peacock Publ.: Frewville, S. Australia). pp. 35-45.
- Carolin, R. C. (1981). A review and critique of studies on the phytogeography of Arid Australia. In Barker, W. R. & Greenslade, P. J. M. (eds), 'Evolution of the Flora and Fauna of Arid Australia'. (Peacock Publ.: Frewville, S. Australia). pp. 119-123.
- Cruden, R. W. (1967a). Intraspecific variation in pollen-ovule ratios and nectar secretion — preliminary evidence of ecotypic adaptation. *Ann. Missouri Bot. Gard.* 63: 277-289.
- Cruden, R. W. (1967b). Fecundity as a function of nectar production and pollen-ovule ratios. In Burley, J. & Styles, B. T. (eds), 'Tropical Trees, Variation, Breeding and Conservation'. (Academic Press: London). pp. 171-178.
- Cruden, R. W. (1977). Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32-46.
- Cruden, R. W. & Hermann-Parker, S. M. (1979). Butterfly pollination of *Caesalpinia pulcherrima*, with observations on a Psychophilous syndrome. *J. Ecol.* 67: 155-168.
- Gibbs, P. E., Milne, C. & Carillo, M. V. (1975). Correlation between the breeding systems and recombination index in five species of *Senecio*. *New Phytol.* 75: 619-626.
- Holmgren, P. K. & Keuken, W. (1974). 'Index Herbariorum. Part 1. The Herbaria of the World' 6 ed. (Oosthoek, Scheltema & Holkema: Utrecht).
- Kyhos, D., Carter, C. R. & Smith-White, S. (1977). The cytology of *Brachycome lineariloba*. 7. Meiosis in natural hybrids and race relationships. *Chromosoma (Berl.)* 65: 81-101.
- Lawrence, M. E. (1985). *Senecio* L. (Asteraceae) in Australia: reproductive biology of a species group found primarily in unstable environments. *Aust. J. Bot.* (in press).
- Lloyd, D. G. (1965). Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). *Contr. Gray Herb.* 195: 3-134.
- Lloyd, D. G. (1972). Breeding systems in *Cotula* L. (Compositae, Anthemideae). 1. The array of monoclinal and declinal systems. *New Phytol.* 71: 1181-1194.
- Merxmüller, H., Leins, P. & Roessler, H. (1977). Inuleae — systematic review. In Heywood, V. H., Harborne, J. B. & Turner, B. L. (eds), 'The Biology and Chemistry of the Compositae'. (Academic Press: London, New York & San Francisco). pp. 577-602.
- Ornduff, R. (1969). Reproductive biology in relation to systematics. *Taxon* 18: 121-133.
- Schoen, D. J. (1977). Morphological, phenological and pollen-distribution evidence of autogamy and xenogamy in *Gilia achilleifolia* (Polemoniaceae). *Syst. Bot.* 2: 280-286.
- Short, P. S. (1981). Pollen-ovule ratios, breeding systems and distribution patterns of some Australian Gnaphaliinae (Compositae: Inuleae). *Muelleria* 4: 395-417.
- Short, P. S. (1983). A revision of *Angianthus* Wendl., sensu lato (Compositae: Inuleae: Gnaphaliinae). *Muelleria* 5: 143-214.
- Spira, T. P. (1980). Floral parameters, breeding system and pollinator type in *Trichostema* (Labiatae). *Amer. J. Bot.* 67: 278-284.
- Stace, H. M. (1981). *Calotis* (Compositae), a Pliocene arid zone genus? In Barker, W. R. & Greenslade, P. J. M. (eds), 'Evolution of the Flora and Fauna of Arid Australia'. (Peacock Publ.: Frewville, S. Australia). pp. 357-367.
- Storey, W. B. & Mann, J. D. (1967). Chromosome contraction by o-isopropyl-N-phenylcarbamate (IPC). *Stain Technol.* 42: 15-18.
- Turner, B. L. (1970). Chromosome numbers in the Compositae. XII. Australian species. *Amer. J. Bot.* 57: 382-389.